Intraspecific variation in an early skeletal metazoan: Namacalathus from the Ediacaran Nama Group, Namibia

Geobiology

Intraspecific variation in an early skeletal metazoan: *Namacalathus* from the Ediacaran Nama Group, Namibia.

Journal:	*Geobiology*
Manuscript ID	GBI-003-2016.R1
Manuscript Type:	Research Article
Key Words:	Ediacaran, Namibia, Metazoan, Palaeoecology

Intraspecific variation in an Ediacaran skeletal metazoan: *Namacalathus* from the Nama Group, Namibia.

ABSTRACT

Namacalathus hermanastes is one of the oldest known skeletal metazoans, found in carbonate settings of the terminal Ediacaran (~550-541 Million years (Ma) ago). The palaeoecology of this widespread, goblet-shaped, benthic organism is poorly constrained yet critical for understanding the dynamics of the earliest metazoan communities.

Analysis of in-situ assemblages from the Nama Group, Namibia (~548-541 Ma), shows that *Namacalathus* exhibited size variation in response to differing water depths, hydrodynamic conditions, and substrate types. In low energy, inner ramp environments, *Namacalathus* attains the largest average sizes but grew in transient, loosely-aggregating, monospecific aggregations attached to microbial mats. In high energy mid-ramp reefs, *Namacalathus* spatially segregated into different palaeoecological habitats with distinct size distributions. In outer ramp environments, individuals were small and formed patchy, dense, monospecific aggregations attached to thin microbial mats. Asexual budding is common in all settings.

We infer that variations in size distribution in *Namacalathus* reflect differences in habitat heterogeneity and stability, including the longevity of mechanically stable substrates and oxic conditions. In the Nama Group, long-lived skeletal metazoan communities developed within topographically heterogeneous mid-ramp reefs which provided diverse mechanically stable microbial substrates in persistently oxic waters, while inner and outer ramp communities were often ephemeral, developing during fleeting episodes of either oxia and/or substrate stability. We conclude that *Namacalathus*, which forms a component of these communities in the Nama Group, was a generalist that adapted to various palaeoecological habitats within a

heterogeneous ecosystem landscape where favourable conditions persisted, and was also able to opportunistically colonise transiently hospitable environments. These early skeletal metazoans colonised previously unoccupied substrates in thrombolitic reefs and other microbial carbonate settings, and while they experienced relatively low levels of inter-specific competition, they were nonetheless adapted to the diverse environments and highly dynamic redox conditions present in the terminal Ediacaran.

INTRODUCTION

Ediacaran (580–541 million years ago) strata yield diverse non-skeletal and skeletal macrofossils which record the emergence of metazoans and complex ecosystems. Many of these forms have unresolved phylogenetic relationships, reproductive modes, and ecologies, even though an understanding of these is critical to investigating the origins of the modern biosphere.

Ediacaran macroorganisms may have been capable of multiple reproductive modes, implying the presence of correspondingly complex developmental systems (Mitchell *et al.*, 2015). The terminal Ediacaran (~550-541 Ma) skeletal taxa *Cloudina* and *Namacalathus* reproduced clonally through budding (Hua *et al.*, 2005; Cortijo *et al.*, 2010; Zhuravlev *et al.*, 2015a), but their broad geographic distribution suggests that like many extant benthic invertebrates, they also possessed a dispersive, planktonic larval stage (Zhuravlev *et al.*, 2012, fig. 7; Cortijo *et al.*, 2015). Size distributions, and bedding plane-scale spatial distributions have further been used to distinguish reproductive styl For example, the unmineralised taxa *Funisia* and *Tribrachidium* cluster into groups of similar size, suggesting episodic larval settlement (Droser & Gehling, 2008; Hall *et al.*, 2015), and *Fractofusus* shows a recurring pattern of smaller individuals clustered around larger ones suggestive of clonal reproduction via stolons (Mitchell *et al.*, 2015).

Namacalathus has a goblet-like morphology, consisting of a hollow stem which flares to form a 'cup'. The cup generally has 6 or 7 lumens in the side walls imparting a polygonal cross-section, and a larger opening at the top whose edges curl in towards a central cavity (Grotzinger *et al.*, 2000; Watters & Grotzinger, 2001). On the basis of this distinctive but simple morphology, *Namacalathus* has been assigned various affinities. It has been interpreted as a possible cnidarian because of its goblet-shaped morphology and hexaradial cross-section (Grotzinger *et al*., 2000), a protozoan due to its small size and an apparent lack of accretionary growth (Seilacher *et al*., 2003), and a stem eumetazoan based on its symmetrical, stalked morphology and sessile, benthic life habit (Wood, 2011). More recently, a lophophorate affinity has been suggested, based on the presence of bilaterally symmetrical budding and a distinctive skeletal ultrastructure of a tripartite microlamellar construction with columnar deflections (Zhuravlev *et al.*, 2015a).

Namacalathus occurs associated with thrombolitic reefs in carbonate inner, mid- and outer ramp settings in the Nama Group, Namibia (Grotzinger *et al*., 2000; Wood, 2011), and thrombolitic reefs in western Canada and Oman (Hofmann & Mountjoy, 2001; Amthor *et al*., 2003). Some fossils putatively attributed to *Namacalathus* are reported from in a mixed clastic-carbonate environment in West Siberia (Kontorovich *et al*., 2008; Grazhdankin *et al*., 2015) and in reefs associated with calcimicrobes in the Altay Sayan Foldbelt, South Siberia, Russia (Terleev *et al*., 2011). Siberian *Namacalathus* differs from all other fossils ascribed to this genus in possessing a phosphatic skeleton, and pores which are much more numerous than the lumens of *Namacalathus* and are distributed randomly across the cup, while in *Namacalathus* they are fairly uniform in number and position on the cup facets (Grazhdankin *et al*., 2015, fig.4g, h, l). It is also an order of magnitude smaller than the smallest *Namacalathus* from the type locality in Namibia, and from other localities globally (0.2 mm against 2 mm), and so its assignment to this genus is questionable.

To date, published studies on *Namacalathus* are mostly restricted to its morphology and biostratigraphic significance while its reproduction, relationship to substrate, environmental preferences, and other ecological traits have received comparatively little attention. Size distribution data may help constrain some of these uncertainties as *Namacalathus* shows notable size variation between localities both locally and globally. In the Nama Group, Namibia, cup diameters range from 2 to 35 mm (Grotzinger *et al*., 2000; Wood, 2011). Maximum cup diameters of 30 mm are reported from Oman (Amthor *et al*., 2003), and 17 mm from Canada (Hofmann & Mountjoy, 2001), giving a global size range from 2 - 35 mm, excluding Siberian forms. In assemblages from the Byng Formation of western Canada, size differences have been used to infer variation between environmental settings, with larger individuals (modal value ~12 mm) occurring in pockets between stromatolite columns and smaller individuals (modal size ~6 mm) in channel fills (Hofmann & Mountjoy, 2001). Grotzinger *et al*. (2000) observed that *Namacalathus* was more abundant on thrombolites than on other substrates, and suggested that *Namacalathus* preferred the firm, elevated substrates provided by thrombolites in the Nama Group of Namibia. Wood (2011) noted that such habitats also appeared to support the largest individuals.

Metazoans, particularly skeletal ones, are strongly influenced by oxygen levels in their environments. The size and abundance of metazoans in modern benthic communities declines with bottom-water oxygen levels, as does biodiversity (e.g. Rhoads & Morse, 1971). Oxygen levels also have an impact on benthic community structure, with communities under sub-oxic conditions showing reduced pelagic-benthic coupling and suppressed community succession (Nilsson & Rosenberg, 2000; Broman *et al*., 2015). At reduced oxygen levels, communities also consist of smaller, shorter-lived species with opportunistic life histories and few predators (Diaz & Rosenberg, 1995; Sperling *et al*., 2013; 2015), and only very few metazoan taxa may live under permanently anoxic conditions (Danovaro *et al*., 2010). In addition to

oxygen level, redox stability plays a role: some metazoans tolerate temporary, but not permanent, anoxia (Bernhard *et al*., 2000; Müller *et al*., 2012). Consequently, both pO_2 and redox stability are likely to have been important controls on the structure of early metazoan communities (Johnston *et al*., 2012; Wood *et al*., 2015).

The terminal Ediacaran Nama Group, Namibia, was deposited under highly dynamic redox conditions, where shallow, inner ramp settings experienced transient oxygenation (Wood *et al*., 2015). These environments supported short-lived and monospecific skeletal metazoan communities of either *Cloudina* or *Namacalathus*. By contrast, microbial (thrombolite) reefs, found in deeper inner- and mid-ramp settings, support more diverse communities of organisms which constructed reefs and aggregations, may have had distinct environmental preferences, and could attain large sizes (Wood *et al*., 2002; Wood & Curtis, 2015). These long-lived reef communities, as well as Ediacaran soft-bodied biotas, are found particularly within transgressive systems, where oxygenation was persistent. A mid-ramp position may have enabled physical ventilation mechanisms for water column oxygenation to operate during flooding and transgressive sea-level rise. In the Nama Group it appears that the stability of oxygenated conditions may have controlled both the distribution and ecology of Ediacaran skeletal metazoan communities (Wood *et al*., 2015).

Here we explore *Namacalathus* size data and substrate relationships in the Nama Group, Namibia, in order to better constrain its environmental preferences and relationship to its substrate. Among other skeletal metazoans, *Namacalathus* colonized carbonate habitats where microbial mats were abundant, in the diverse environments presented by the late Ediacaran Nama Group. This raises the question of whether the earliest skeletal metazoans were generalists able to colonise a range of environments, or specialists requiring a narrow range of environmental conditions. We place size data within the context of hydrodynamic setting, substrate type and relative redox stability to explore local environmental controls on

early metazoan life habits and ecosystems. Such an analysis contributes to the ongoing discussion of the role of environmental conditions and substrate types in controlling the evolution and palaeoecology of Ediacaran metazoans.

GEOLOGICAL SETTING

The Nama Group (~550 – 541 Ma) is a terminal Ediacaran succession comprising a foreland basin infill of marine shelf and fluvial deposits (Saylor *et al*., 1995). Fossiliferous successions consist of mixed clastics and carbonates ranging from supratidal to outer ramp settings with varying hydrodynamic conditions (Germs, 1995; Jensen *et al*., 2000; Geyer, 2005; Grotzinger & Miller, 2008).

The Nama Group was deposited across the Zaris and Witputs sub-basins (Fig. 1), which have been correlated using a combination of sequence stratigraphy and chemostratigraphy (Figs. 2 and 3) (Saylor *et al*., 1995; 1998). Carbon isotope measurements indicate that the lower Nama Group was deposited during the final stages of the Shuram-Wonoka carbon isotope excursion (Kaufman *et al*., 1991; Wood *et al*., 2015).

Zircons from ash beds in the Nama Group have provided radiometric dates (Fig. 2). The earliest, dated to 547.32 ± 0.65 Ma, is in the Hoogland Member of the Kuibis Subgroup (Grotzinger *et al*., 1995; revised by Schmitz, 2012), and provides a minimum age for the base of the Nama Group. The age of the underlying base of the Nama Group is less certain, but is estimated at around 550 – 553 Ma based on assumed sedimentation rates (Ries *et al*., 2009). An intermediate date of 542.68 ± 1.245 Ma was obtained from an ash bed in the lower Spitskopf Member of the Urusis Formation of the Schwarzrand Subgroup (Grotzinger *et al*. 1995; Schmitz, 2012). The youngest Ediacaran ash bed in the Nama Group, 130 m below the youngest *Cloudina* and unmineralised Ediacaran fossils, but above the stratigraphically highest *Namacalathus* assemblage in this study gave U-Pb dates of 540.61 ± 0.67 Ma in the

upper Spitskopf Member (Grotzinger *et al*., 1995 as 543.3 ± 1 Ma; date recalculated by Schmitz, 2012). A fourth ash bed in the lower Nomtsas Formation, above the unconformity that includes the Precambrian-Cambrian boundary, gave an estimated date of 538.18 ± 1.24 Ma, giving a minimum age for the Precambrian-Cambrian boundary in the Nama Group (Grotzinger *et al*., 1995; Schmitz, 2012). The localities in this study therefore span ≥ 6 Myr from the Lower Omkyk Member (> 547 Ma) to the Spitskopf Member (~ 541 Ma).

Environmental and redox settings of localities

Namacalathus assemblages were studied at five localities which represent three environments: Low energy inner ramp, high energy mid-ramp thrombolitic reefs, and low energy outer ramp (Table 1, Figs. 2 and 3, for locality coordinates, see Table SM 1). Below, we briefly document the sedimentology, and outline the redox dynamics of each setting. Redox conditions for each of these localities has been inferred by Wood *et al*. (2015) based on a multiproxy approach using iron speciation (Fe_{HR}/Fe_T), total iron (Fe_T), and Fe/Al ratios, summarised in Table 1; for an explanation of the proxies see Table SM 2.

The use of geochemical proxies to explain biological patterns requires reconciliation of markedly different time scales of integration. Biological time scales, such as the time between successive generations are often short compared with the geological timescales over which sediment accumulates and geochemical signatures develop (Wood *et al*., 2015). In addition, iron speciation may not be sufficiently sensitive to detect whether pO_2 was above or below the crucial thresholds for metazoan life (Sperling *et al*., 2013). With care, however, geochemical proxies may be used to make inferences on local-scale palaeoenvironmental dynamics (Hall *et al*., 2013; Wood *et al*., 2015; Sperling *et al*., 2015; Jin *et al*., 2016).

The low energy inner ramp setting in the Omkyk Member is dominated by dolomitised micritic, laminated lithologies, with thinly bedded (~10-100 mm thickness) mudstones,

wackestones and packstones, which accumulated mainly during sea level highstands. Thin, closely-spaced, undulating laminae suggest that thin microbial mats developed regularly, binding fine grained sediment. Fe_{HR}/Fe_T, Fe_T and Fe/Al data show that such settings experienced only intermittent oxia, and benthic metazoan communities developed during these fleeting oxic episodes (Wood *et al.*, 2015). Some beds with clearly in-situ *Namacalathus* assemblages nonetheless present an anoxic iron speciation signature, even when microsampled (Wood *et al.,* 2015). From this it has been inferred that the transient populations exploited brief periods of oxia in otherwise dominantly and more persistently anoxic settings, which may have been caused by periodic upwelling of anoxic deep waters (Wood *et al.*, 2015).

Mid-ramp thrombolitic reefs in the Omkyk Member are associated with packstones, cross-bedded grainstones and breccias that developed during transgressive systems tracts in relatively energetic waters. These microbial reef complexes range from a few metres to kilometres in extent. Variable *Namacalathus* ecology has been documented from these reefs, and includes attachment to thrombolite heads (Grotzinger *et al*., 2000; Wood, 2011), growth as monospecific sheet-like aggregations, intergrowth with *Cloudina riemkeae* thickets, and growth within primary cavities (crypts) in thrombolitic reefs (Wood & Curtis, 2015). The very low Fe_T of mid-ramp reef settings suggest that these were probably persistently oxic, especially during transgressive systems tracts, when large microbial reefs with calcified metazoan communities developed.

Swartpunt locality from the Spitskopf Member of the Schwartzrand Subgroup is interpreted as an outer ramp setting. Although the succession shallows to inner ramp environments, the sampled lower part of the succession is dominated by laterally continuous to discontinuous thin- to medium bedded (50-150 mm) wackestones and packstones. Some units show scoured bases and low relief channels. We infer deposition below fair weather

wave base, under weak current activity and occasional disturbance by storms. Thin, undulating, irregularly spaced laminae suggest that thin microbial mats developed intermittently, binding fine micritic or fine grain sediment. Very low Fe_T suggests that these settings were probably deposited in oxic waters (Wood *et al*., 20

Size data were sub-divided by locality and setting, and individuals from mid-ramp reefs were further sub-divided into three palaeoecological habitats: those found adjacent to thrombolite heads, those in low-relief sheets on open surfaces, and those found within reef crypts. On the basis of these differing habitats, we infer that *Namacalathus* occupied different specific areas within the overall metazoan-microbial ecosystem. In sum, we identify five palaeoecological habitats: Low energy inner ramp, Mid-ramp reef: Thrombolite association, Mid-ramp reef: Open surface sheet, Mid-ramp reef: Cryptic (occupying reef crypts), and Outer ramp.

METHODS

Namacalathus fossils were identified as in life position on the basis of intact skeletons with an upwards growth perpendicular to bedding planes. Some show skeletal deformation due to close-packed growth, or show the base of the stem anchored in sediment or attached to microbial mats. Measurements were taken from scans of rock samples, and from field photographs, and the cup diameter of in-situ *Namacalathus* individuals was recorded (see Table SM 7).

Because of the three-dimensional preservation of *Namacalathus* in the Nama Group, exposed or cut rock surfaces present a variety of different sections through the skeleton due to variations in the orientation of individuals relative to exposed rock surfaces. Consequently, a complete set of measurements is impossible on most *Namacalathus* individuals. However, cup diameter is commonly measurable, so has been used as a size indicator. Field

photographs and scans of rock specimens were imported into ImageJ for data collection, and measurements were made from all clearly visible individuals in each image; specimens where cup diameter could not be measured or identification as *Namacalathus* was not certain were excluded.

Different sections through the skeleton were categorised into 'vertical', 'horizontal' and 'oblique' as the type of section measured can alter the apparent size. 'Vertical', 'horizontal' and 'oblique' sections are defined as follows: 'vertical' sections represent a slice parallel to the growth axis of the fossil which includes both the apical opening in the cup and the hole at the base of the stem. 'Horizontal' sections through the cup are perpendicular to the growth axis and preserve the outer wall of the cup together with the 5-7 lateral lumens. 'Oblique' sections are any other section through the apical cup. An oblique section through a goblet shape is likely to show a smaller cup diameter than a vertical or horizontal section.

Vertical and horizontal sections are most useful as they permit a consistent comparison of measurements between individuals. However, oblique sections are also useful as they provide a minimum size constraint, so they have been included in this analysis. Maximum measured cup diameter at each site may also usefully reflect size differences between palaeoecological habitats, although is not amenable to statistical testing. When describing *Namacalathus* assemblages, we therefore use the median for statistical purposes (for a justification of this, see the Shapiro-Wilk normality test in Results section), but also quote the maximum cup diameter.

Where vertical sections were available, both cup diameter and cup height measurements were taken (see Table SM 8), to determine whether *Namacalathus* individuals in different settings shared a growth trajectory. Since vertical sections, which are required for cup height measurements, are much rarer than oblique ones, this dataset is much smaller than the cup diameter dataset and consequently has not been subjected to the same statistical analyses. In

total, 398 sections were measured, of which 97 were vertical; there are five vertical sections for which cup height was not measured due to breakage at the apical part of the cup. For all statistical tests, p-values lower than 0.05 were taken as significant. Statistical tests were performed in PAST, version 3.02 (Hammer, 2014), and in R.

To determine whether the cup diameter data were normally distributed, and inform further statistical tests, a Shapiro-Wilk test was applied to the data from each of the five palaeoecological habitats, and to the dataset as a whole. The Shapiro-Wilk test was selected due to its statistical power, and was first applied to the raw data, then to the log-transformed dataset. In the Shapiro-Wilk test, the null hypothesis (H_0) is that the data were taken from an assemblage with a normal distribution.

The Kolmogorov-Smirnov test was used to compare the overall cup diameter distribution across all data with the distributions in each of the five palaeoecological habitats (Table SM 5). The Kolmogorov-Smirnov test is a pairwise non-parametric test which detects differences in both the shape and position of a distribution, and was selected because it makes no assumptions about the distribution of the data, and its application in this way avoids multiple comparisons problems which can lead to Type 1 errors. In the Kolmogorov-Smirnov test, the null hypothesis (H_0) is that the two samples under comparison come from assemblages with the same distribution.

To compare the median cup diameter values from each dataset, a Kruskal-Wallis test was performed. The Kruskal-Wallis test is a multiple samples test whose null hypothesis (H_0) is that there is no statistically significant difference between the medians of the samples. The test was selected because it does not require an assumption that the data are normally distributed.

Although the results of the Kruskal-Wallis test do not identify the sources of statistically significant differences in the median between samples, this can sometimes be ascertained by

visually comparing the data distributions of the samples. However, Mann-Whitney tests were also carried out on all possible pairs of palaeoecological habitats to ascertain where statistically significant differences in the median lay, as data from some palaeoecological habitats gave visually similar distributions. In the Mann-Whitney test, the null hypothesis (H_0) is that there is no significant difference between the medians of two samples. A Bonferroni correction was applied to remedy the potential problem of multiple comparisons leading to Type 2 errors (i.e. falsely identifying significant differences). A linear regression was used to determine if the cup diameter and cup height of all vertical sections correlated, with the aim of determining if they had a shared growth trajectory. A Spearman's Rank correlation coefficient (r_s) was also calculated to quantify the correlation, and was selected because it makes no assumptions about data distribution. If $r_s = 1$ or -1, there is a perfect monotonic relationship between the two variables (in this case, cup height and cup diameter).

RESULTS

Aggregation Style

Namacalathus commonly occurs in densely aggregated assemblages which range from decimetre to metre scale. In the inner ramp setting, some in-situ *Namacalathus* occur as isolated individuals (Fig. 4A, C), but most are found in aggregations of up to 0.5 m diameter (Fig. 4B).

In mid-ramp reefs, small (<0.5 m) aggregations are associated with thrombolite heads. These close-packed aggregations contain individuals of up to 35 mm cup diameter, though a range of individual sizes occurs (Fig. 5A, B, F). Some of these large individuals also have external spines, though the sample contains too few individuals with this feature to statistically analyse its occurrence (Fig. 5B). On open surfaces in mid-ramp reefs, *Namacalathus* aggregates to form sheets of up to 5 m in diameter (Fig. 5D, G), and also

intergrows with extensive (> 20 m in diameter) thickets of *Cloudina riemkeae* (Fig. 5E, D, Wood & Curtis, 2015). One open surface aggregation appeared to contain individuals whose cups are slightly ellipsoidal, with a preferential orientation to their long axes, though the sample is small (Figs. SM 1, 2); however, oblique sectioning of a uniformly oriented assemblage of in-situ fossils cannot be discounted. The small available sample size for the cryptic habitat does not permit an assessment of aggregation style (Fig. 5C).

In the low energy outer ramp, small lenticular aggregations (<0.3 m diameter) occur (Fig. 6A, C, D). These aggregations develop very little topographic relief, and may occupy scours produced by periodic storms.

Cup Diameter

In total, 398 individuals were measured, and of these 97 were represented by a vertical section through the skeleton, 12 by horizontal sections, and 289 by oblique sections. Cup diameter data are given in Table SM 7.

The Shapiro-Wilk test returned a p-value of 9.156E-16 when applied to the whole cup diameter dataset, and 0.003318 when applied to the log-transformed dataset, implying that the data do not show a normal or log-normal distribution overall. Histograms of the cup diameter data were also plotted to give a visual indication of the data distribution (Fig. 7). These show a highly non-normal distribution, with most individuals tending towards the smaller end of the size scale. This distribution persists whether the whole cup diameter dataset is plotted, or just data from vertical and horizontal sections, which we might expect to reflect true cup diameter more accurately.

The results of the Shapiro-Wilk test on cup diameter datasets from each of the five palaeoecological habitats are given in the Supplemental Material (Table SM 3). All returned p-values below 0.05, so we reject the null hypothesis that the cup diameter data are normally

distributed. In the case of the outer ramp locality, the p-value returned was 0.049, very close to the critical value but still below it.

The Shapiro-Wilk test was repeated on the log-transformed cup diameter data for each palaeoecological habitat, returning p-values over 0.05 (Table SM 4) we cannot reject the null hypothesis that the log-transformed data from each palaeoecological habitat are normally distributed.

Since the untransformed cup diameter data are not normally distributed, the median was used for comparison of central tendency between habitats (Fig. 8A). Inner ramp individuals have the largest median cup diameter (8.0 mm) and also show a larger range of cup diameters than the outer ramp. The outer ramp showed the smallest median cup diameter (4.4 mm), and the smallest range. In mid-ramp reefs, individuals from the three distinct habitats have different cup diameter ranges. Individuals associated with thrombolite heads have a median cup diameter of 7.7 mm. Those growing on open surfaces or intergrown with *Cloudina riemkeae* had a median cup diameter of 6.9 mm, and individuals in reef crypts have a median cup diameter of 5.8 mm.

Non-parametric tests were applied to the untransformed cup diameter data to assess the statistical significance of differences between size distributions. Kolmogorov-Smirnov tests were applied to *Namacalathus* cup diameter datasets from each palaeoecological habitat, to compare them with the overall cup diameter distribution for all data. Results are tabulated in Supplementary Materials (Table SM 5). For all palaeoecological habitats except for the mid-ramp reef open surface, the Kolmogorov-Smirnov test returned a p-value lower than 0.05, so we may reject the null hypothesis that cup diameter distributions within the other palaeoecological habitats match the overall distribution of the data.

The Kruskal-Wallis test returned a p-value of 2.9E-19, so we reject the null hypothesis that there is no significant difference in the median cup diameter of samples from each of the

five palaeoecological habitats. Bonferroni corrected p-values resulting from the Mann-Whitney tests on all pairs of samples are given in Table SM 6, and vary from p = 1.43E-15 (for the comparison of the outer ramp with low energy inner ramp palaeoecological habitats) to p = 1 (for the comparison of the low energy inner ramp and mid-ramp reef thrombolite associated samples).

According to the Mann-Whitney tests, the median cup diameter in the low energy inner ramp palaeoecological habitat was significantly different to that of all other palaeoecological habitats (p-values of 1.43E-15 to 0.01665) except to that of the mid-ramp reef thrombolite association, which returned a p-value of 1. Within the mid-ramp reef setting, there was no significant difference between the median cup diameters of the open surface, thrombolite-associated and cryptic palaeoecological habitats (p-values of 0.1195 to 0.4417), though the open surface and cryptic palaeoecological habitats hosted *Namacalathus* with a significantly different median cup diameter to the low energy inner ramp and outer ramp habitats (p-values of 6.07E-14 to 0.01665). Finally, the outer ramp *Namacalathus* assemblage had a significantly different median cup diameter to the assemblages from all other palaeoecological habitats (p-values of 1.43E-15 to 0.005758).

Though not amenable to statistical analysis, maximum cup diameter may also be informative due to the prevalence of oblique sections in our dataset. Inner ramp individuals have a maximum cup diameter of 23.7 mm, while in the mid-ramp reef environment, individuals in cryptic environments had a maximum cup diameter of 12 mm, those on open surfaces 18.4 mm, and in thrombolite associations 35.1 mm. Outer ramp settings show the smallest maximum cup diameter at 8.9 mm.

To check whether all individuals in the dataset shared a growth trajectory, cup height was plotted against cup diameter for 92 vertical sections from the entire dataset, regardless of habitat. Spearman's Rank correlation coefficient (r_s) returned a value of 0.84506, suggesting

a correlation between the two. A major axis linear regression model was fitted to the data and visual inspection shows that that cup height appears to be proportional to cup diameter across all data (See Fig. 8B).

Relationship to substrate

In the inner and outer ramp settings, *Namacalathus* is anchored to or within thin microbial laminae by the base of the stem, occupying small primary depressions in the surface of the microbial laminae (Figs. 4C and 6B, D). By contrast, mid-ramp settings provided thrombolitic substrates. While direct contact between the bases of stems and thrombolite surfaces was not observed in the mid-ramp reefs, early cements encase the erect *Namacalathus* individuals, suggesting that they are in life position. Forms in reef crypts are also attached to thrombolitic substrates (Fig. 5C). The attachment of the sheet-like aggregations is not clear, but these may be attached to *Cloudina riemkeae* thickets intergrown with thrombolite (Wood & Curtis, 2015).

Budding distribution

Regular bilateral budding in *Namacalathus* was reported in the outer ramp (Figs. 6D and E) and inner ramp (Fig. 4B) (Zhuravlev *et al*. 2015a). In contrast, smaller individuals are sometimes apparently randomly attached to the inner or outer cup surfaces of larger individuals in mid-ramp thrombolites (Fig. 5A). This may reflect attachment to the pre-existing abandoned skeletons of other individuals.

In the inner ramp, budding is common (Fig. 4B) and smaller individuals also frequently occur within larger forms. In the mid-ramp setting the skeletal continuity between individuals observed in open surface assemblages is suggestive of budding. In the thrombolite-associated setting, one or more small individuals are observed inside the cup of larger individuals,

apparently attached (Fig. 5A). Individuals in reef crypts exhibited no budding, though the sample size here is small.

In the outer ramp, *Namacalathus* forms small, dense aggregations with individuals commonly displaying budding. Here, two possible generations of buds are noted on some individuals (Fig. 6D, E)

DISCUSSION

Namacalathus occupied diverse carbonate settings in terms of water depth, hydrodynamic energy, and variable microbial substrate types (Fig. 9), and *Namacalathus* from different palaeoecological habitats show distinct size distributions (Fig. 8B). However, cup diameter and cup height data correlate across all settings, suggesting that all *Namacalathus* individuals shared the same growth trajectory (Fig. 8B). This implies that they belong to one taxon showing considerable intraspecific size variation, rather than *Namacalathus* in different settings representing different species with distinct environmental preferences. Since size in metazoans is influenced by a variety of factors, many of which are not amenable to explanation using the environmental factors discussed identified here, we will not attempt to assign particular environmental causes to the differences in median cup diameter between palaeoecological habitats. Quantifying size and comparing size distributions can, however, yield information on the adaptations of metazoans to their environments.

Namacalathus attains the largest median cup diameter and a large size range (3.6 – 23.7 mm) within aggregations in the low energy inner ramp environment, though does not attain the maximum sizes found in mid-ramp reef thrombolite-associated individuals (35.1 mm). Statistically, there is no significant difference between the median cup diameters of *Namacalathus* assemblages in the low energy inner ramp and the mid-ramp reef. In the inner ramp settings, thin microbial mats were preferentially colonised, and despite geochemical

evidence for only transient oxygenation on geological timescales, there is evidence of budding which implies that multiple generations developed on the same sites.

In the mid-ramp reef setting, *Namacalathus* occupied at least three palaeoecological habitats, though these assemblages show no statistically significant differences in cup diameter. *Namacalathus* assemblages from each habitat do however show substantial differences in maximum cup diameter and differing size distributions, as well as occupying differing substrates. Individuals in depressions between microbialite mounds attained the largest maximum sizes (Grotzinger *et al*. 2000; Hofmann & Mountjoy, 2001; Wood, 2011), while individual sizes show a large range and the attachment of smaller individuals to larger ones suggests that multiple generations were present. The low-relief open surface assemblages do not show a cup diameter distribution that differs significantly from the cup diameter distribution across the whole dataset, but the cup diameter distribution of the assemblage in reef crypts does differ significantly from the overall distribution, likely because of their smaller cup diameters and smaller size range (Fig. 8A). We suggest that persistently oxic conditions and the range of varied, mechanically stable substrates in such topographically complex habitats may have allowed occupancy of a wider range of substrates over longer timescales.

By contrast, the inner and outer ramp environments lack any differentiation into different habitats, which may in part reflect the lack of topographic heterogeneity offered in these settings compared with mid-ramp reefs. The outer ramp *Namacalathus* individuals are generally much smaller than those in the inner or mid-ramp, though the presence of budding or multiple generations suggests that the outer ramp hosted assemblages of mature, reproducing individuals. Nontheless, *Namacalathus* in transiently hospitable inner and outer ramp settings may still have experienced early mortality or shown high growth rates. This may be compared to modern populations which show an adaptive response to stressful

conditions resulting in early growth cessation and reproductive onset combined with early and high adult mortality (Perry & Dominy, 2009; Whiteman *et al*., 2012). Regardless, it appears that *Namacalathus* was adapted for life in transiently hospitable environments.

In modern ecosystems, species that first colonise newly available heterogeneous landscapes in the absence of strong intra-specific competition, e.g., fishes in postglacial lakes, often establish co-existing sympatric morphotypes (Rundle *et al*., 2000; Klemetsen, 2010). These can show remarkably different sizes, mouth parts, and behaviour within single lakes even in the absence of reproductive isolation because such morphs are adapted to different resource niches (Klemetsen, 2010). While there are few studies on low-competition benthic metazoan communities, high rates of sympatric speciation are observed among benthic caenogastropods of the East African Great Lakes due to phenotypic plasticity which in turn reflect a rising opportunity for ecophenotypes to occupy different substrates (Salzburger *et al.,* 2014). It is possible that carbonate settings in the late Ediacaran presented a similar landscape of low competition with a limited number of metazoan species forming low diversity communities. This may have promoted the intraspecific size variation of *Namacalathus* noted here, allowing differentiation into morphs of different sizes due to adaptation to various substrates, relative redox stability or variable hydrodynamic conditions. This is particularly evident in the difference in median cup diameter between the outer ramp *Namacalathus* and those in the rest of the dataset.

Size differentiation may indicate intraspecific niche partitioning, particularly in mid-ramp reefs, whereby natural selection drives members of a species into different sub-groupings according to different patterns of resource use or niches. Alternatively, the differences in size distribution may represent intraspecific ecophenotypic variation - a phenomenon well-documented in sessile benthic metazoans (e.g. Alexander, 1975; Scrutton, 1996; Gittenberger & Hoeksema, 2006; Zieritz & Aldridge, 2009).

Namacalathus appears to have been an environmental generalist, occupying a range of different settings from inner ramp lagoons to more distal ramp environments, and both open surface and cryptic habitats in mid-ramp reefs. It was capable of high intraspecific size variation, and may have differentiated into size morphs. Variable redox conditions and otherwise transiently available habitats appear not to have been a barrier to growth and reproduction despite *Namacalathus*' presumed reliance on oxygen for maintenance of metabolism. A tendency towards opportunistically colonising areas during transient periods of oxia would have served *Namacalathus* well in the Nama Group in the late Ediacaran, and it is possible that this was a widespread ecological strategy among Ediacaran skeletal metazoans.

This highly generalist behaviour whereby *Namacalathus* occupied different microenvironments via intraspecific variation and possibly the development of different size morphs adapted to local conditions contrasts with the next phase of sessile calcified metazoan development, represented by the lower Cambrian Stage 2 (~535 – 525 Ma) archaeocyathan reefs of the Siberian Platform. Here, different microenvironments were occupied by specialised representatives of different species and genera (Zhuravlev & Wood, 1995; Debrenne & Zhuravlev, 1996; Zhuravlev, 2001; Zhuravlev *et al*., 2015b). As such, we may infer an escalation in levels of inter-specific competition in sessile skeletal metazoans from ~548 to 535 Ma.

CONCLUSIONS

Namacalathus occupied a variety of palaeoenvironments in the Nama Basin, and exhibited intraspecific size variation between settings. The largest individuals lived in association with mid-ramp reef thrombolites, while the smallest lived in cryptic habitats in mid-ramp reefs, and in more distal ramp environments. In mid-ramp reefs, *Namacalathus* occupied a range of

habitats, and formed large, persistent aggregations in association with other early skeletal metazoans. This is likely to be due to the mechanical stability of substrates and persistence of oxic waters in this habitat.

We conclude that *Namacalathus* was an environmental generalist that colonised both persistently and transiently oxic habitats, and spatially differentiated into populations with differing size distributions. As such, *Namacalathus* was adapted to the various substrates and sometimes highly dynamic redox environment that characterized the late Ediacaran Nama Group. This contrasts with the situation in early Cambrian metazoan reefs, whereby individual taxa were specialised for particular microenvironments, and may reflect a trend from generalist to specialist in the earliest sessile metazoans of shallow marine carbonate settings.

ACKNOWLEDGEMENTS

AP is grateful for funding from a University of Edinburgh, School of Geosciences Scholarship and the International Centre for Carbonate Reservoirs. RW, RT, and AP acknowledge support from NERC through the 'Co-evolution of Life and the Planet' scheme. FB thanks the Laidlaw Hall Trust for fieldwork support. We thank the Geological Survey of Namibia, and A. Horn of Omkyk, L. and G. Fourie of Zebra River, C. Husselman of Driedoornvlagte, and L. G'Evereet of Swartpunt for access to their farms, and Mike Hall for technical support. We also thank Duncan Murdock, Marc Laflamme and five anonymous reviewers for their insightful and constructive comments.

REFERENCES CITED

Alexander RR (1975) Phenotypic lability of the brachiopod *Rafinesquina alternata* (Ordovician) and its correlation with the sedimentologic regime. *Journal of Paleontology*, **49**, 4, 607-618

Amthor JE, Grotzinger JP, Schröder S, Bowring SA, Ramezani J, Martin MW, Matter A (2003) Extinction of *Cloudina* and *Namacalathus* at the Precambrian-Cambrian boundary in Oman. *Geology*, **31**, 431-434.

Bernhard JM, Buck KR, Farmer MA, Bowser SS (2000) The Santa Barbara Basin is a symbiosis oasis. *Nature* **403**, 77-80.

Broman E, Brüsin M, Dopson M, Hylander S (2015) Oxygenation of anoxic sediments triggers hatching of zooplankton eggs. *Proceedings of the Royal Society B*, **282**, 1817, 20152025.

Cortijo I, Martí Mus M, Jensen S, Palacios T (2010) A new species of *Cloudina* from the terminal Ediacaran. *Precambrian Research* **176**, 1-10.

Cortijo I, Cai Y, Hua H, Schiffbauer JD, Xiao S (2015) Life history and autoecology of an Ediacaran index fossil: Development and dispersal of *Cloudina*. *Gondwana Research* **28**, 419-424.

Danovaro R, Dell'Anno A, Pusceddu A, Gambi C, Heiner I, Kristensen RM (2010) The first metazoa living in permanently anoxic conditions. *BMC Biology* **8**, 30.

Debrenne F, Zhuravlev AYu (1996) Archaeocyatha, palaeoecology: a Cambrian sessile fauna. *Bollettino della Societa Paleontologica Italiana, Special Volume*, **3**, 77-85.

Diaz RJ, Rosenberg R (1995) Marine benthic hypoxia: A review of its ecological effects and the behavioural responses of benthic macrofauna. *Oceanography and Marine Biology: an Annual Review*, **33**, 245-303.

Droser ML, Gehling JG 2008. Synchronous Aggregate Growth in an Abundant New Ediacaran Tubular Organism**.** *Science* **319,** 1660-1662.

Germs GJB (1995) The Neoproterozoic of southwestern Africa, with emphasis on platform stratigraphy and paleontology. *Precambrian Research*, **73**, 137-151.

Geyer G (2005) The Fish River Subgroup in Namibia: stratigraphy, depositional environments and the Proterozoic-Cambrian boundary problem revisited. *Geological Magazine*, **142**, 5, 465-498.

Gittenberger A, Hoeksema BW (2006) Phenotypic plasticity revealed by molecular studies on reef corals of *Fungia* (*Cycloseris*) spp. (Scleractinia: Fungiidae) near river outlets. *Contributions to Zoology*, **75** (3/4), 195-201.

Grazhdankin DV, Kontorovich AE, Kontorovich VA, Saraev SV, Filippov Yu F, Efimov AS, Karlova GA, Kochnev BB, Nagovitsin KE, Terleev AA, Fedyanin GO (2015) Vendian of the Fore-Yenisei sedimentary basin (*southeastern West Siberia*). *Russian Geology and Geophysics*, **56**, 560-572.

Grotzinger JP, Bowring SA, Saylor BZ, Kaufman AJ (1995) Biostratigraphic and Geochronologic Constrains on Early Animal Evolution. *Science, New Series*, **270**, 5236, 598-604.

Grotzinger JP, Watters WA, Knoll AH (2000) Calcified metazoans in thrombolite-stromatolite reefs of the terminal Proterozoic Nama Group, Namibia. *Paleobiology*, **26**, 3, 334-359.

Grotzinger JP, Miller RMcG (2008) Nama Group. In: *The Geology of Namibia, v. 2* (ed. Miller, R McG). Geological Survey of Namibia, pp. 13.229-13.272.

Hall M, Kaufman AJ, Vickers-Rich P, Ivantsov A, Trusler P, Linnemann U, Hofmann M, Elliott D, Cui H, Fedonkin M, Hoffmann K-H, Wilson S, Schneider G, Smith J (2013) Stratigraphy, palaeontology and geochemistry of the late Neoproterozoic Aar Member, southwest Namibia: Reflecting environmental controls on Ediacara fossil

preservation during the terminal Proterozoic in African Gondwana. *Precambrian Research* **238**, 214-232.

Hall CMS, Droser ML, Gehling JG, Dzaugis ME (2015) Paleoecology of the enigmatic *Tribrachidium*: New data from the Ediacaran of South Australia. *Precambrian Research* **269**, 183-194.

Hammer Ø (2014) PAST, PAleontological STatistics, version 3.02.

Hofmann HJ, Mountjoy EW (2001) *Namacalathus-Cloudina* assemblage in Neoproterozoic Miette Group (Byng Formation), British Columbia: Canada's oldest shelly fossils. *Geology*, **29**, 1091-1094.

Hua H, Chen Z, Yuan X, Zhang L, Xiao S (2005) Skeletogenesis and asexual reproduction in the earliest biomineralizing animal *Cloudina*. *Geology* **33**, 277-280.

Jensen S, Saylor BZ, Gehling JG, Germs GJB (2000) Complex trace fossils from the terminal Proterozoic of Namibia. *Geology*, **28**, 143-146.

Jin C, Li C, Algeo TJ, Planavsky NJ, Cui H, Yang X, Zhao Y, Zhang X, Xie S (2016) A highly redox-heterogeneous ocean in South China during the early Cambrian (~529-514 Ma): Impications for biota-environment co-evolution. *Earth and Planetary Science Letters* **441**, 38-51.

Johnston DT, Poulton SW, Goldberg T, Sergeev VN, Podkovyrov V, Vorob'eva NG, Bekker A, Knoll AH (2012) Late Ediacaran redox stability and metazoan evolution. *Earth and Planetary Science Letters* 335-336: 25-35.

Kaufman AJ, Hayes JM, Knoll AH, Germs GJB (1991) Isotopic compositions of carbonates and organic carbon from upper Proterozoic successions in Namibia: stratigraphic variation and the effects of diagenesis and metamorphism. *Precambrian Research*, **49**, 301-327.

Klemetsen A (2010) The charr problem revisited: exceptional phenotypic plasticity promotes ecological speciation in postglacial lakes. *Freshwater Reviews*, **3**, 49-74.

Kontorovich AE, Varlamov AI, Grazhdankin DV, Karlova GA, Klets AG, Kontorovich VA, Saraev SV, Terleev AA, Belyaev SYu, Varaksina IV, Efimov AS, Kochnev BB, Nagovitsin KE, Postnikov AA, Filippov YuF (2008) A section of Vendian in the east of West Siberian Plate. *Russian Geology and Geophysics*, **49**, 932-939.

Mitchell EG, Kenchington CG, Liu AG, Matthews JJ, Butterfield NJ (2015), Reconstructing the reproductive mode of an Ediacaran macro-organism. *Nature* 524, 7565, 343-346.

Müller M, Mentel M, van Hellemond JJ, Henze K, Woehle C, Gould SB, Yu R-Y, van der Giezen M, Tielens AGM, Martin WF (2012) Biochemistry and evolution of anaerobic energy metabolism in eukaryotes. *Microbiology and Molecular Biology Reviews* **76**, 2, 444-495.

Nilsson, HC, Rosenberg, R (2000) Succession in marine benthic habitats and fauna in response to oxygen deficiency: analysed by sediment profile-imaging and by grab samples. *Marine Ecology Progress Series* **197**, 139-149.

Perry GH, Dominy NJ (2009) Evolution of the human pygmy phenotype. *Trends in Ecology & Evolution* **24**, 218-225.

Rhoads DC, Morse JW (1971) Evolutionary and ecologic significance of oxygen-deficient basins. *Lethaia*, **4**, 413–428.

Ries JB, Fike DA, Pratt LM, Lyons TW, Grotzinger JP (2009) Superheavy pyrite ($\delta^{34}S_{pyr}$ > $\delta^{34}S_{CAS}$) in the terminal Proterozoic Nama Group, Southern Namibia: A consequence of low seawater sulfate at the dawn of animal life. *Geology* **37**, 8, 743-746.

Rundle HD, Nagel L, Boughman JW (2000) Natural selection and parallel speciation in sympatric sticklebacks. *Science*, **287**, 306-307.

Salzburger W, Van Bocxlaer B, Cohen AS (2014) Ecology and evolution of the African Great Lakes and their faunas. *Annual Review of Ecology, Evolution, and Systematics* **45**, 519-45.

Saylor BZ, Grotzinger JP, Germs GJB (1995) Sequence stratigraphy and sedimentology of the Neoproterozoic Kuibis and Schwarzrand Subgroups (Nama Group), southwestern Namibia. *Precambrian Research*, **73**, 153-171.

Saylor BZ, Kaufman AJ, Grotzinger JP, Urban F (1998) A composite reference section for terminal Proterozoic strata of southern Namibia. *Journal of Sedimentary Research*, **68**, 1223-1235.

Schmitz MD (2012) Radiogenic Isotope Geochronology. In: *Geologic Time Scale 2012*, (ed. Gradstein, FM, Ogg, JG, Schmitz, MD, Ogg, GM), Elsevier, p. 115-126.

Scrutton CT (1996) Ecophenotypic variation in the early Silurian rugose coral *Palaeocyclus porpita*. *Proceedings of the Yorkshire Geological Society* **51**, 1, 1-8.

Seilacher A, Grazhdankin D, Legouta A (2003) Ediacaran biota: the dawn of animal life in the shadow of giant protists. *Paleontological Research*, **7**, 43–54.

Sperling EA, Frieder CA, Raman AV, Girguis PR, Levin LA, Knoll AH (2013) Oxygen, ecology and the Cambrian radiation of animals. *Proceedings of the National Academy of Sciences* **110**, 33, 13446-51.

Sperling EA, Carbone C, Strauss JV, Johnston DT, Narbonne GM, Macdonald FA (2015) Oxygen, facies, and secular controls on the appearance of Cryogenian and Ediacaran body and trace fossils in the Mackenzie Mountains of northwestern Canada. *Geological Society of America Bulletin* B31329-1.

Sperling EA, Knoll AH, Girguis PR (2015) The Ecological Physiology of Earth's Second Oxygen Revolution. *Annual Review of Ecology, Evolution, and Systematics* **46** 215-235.

Terleev AA, Postnikov AA, Tokarev DA, Sosnovskaya OV, Bagmet GN (2011) *Cloudina-Namacalathus-Korilophyton* association in the Vendian of the Altay-Sayan Foldbelt (Siberia). In: *Neoproterozoic sedimentary basins: stratigraphy, geodynamics and petroleum potential*. Proceedings of the International Conference (Novosibirsk, 30 July - 02 August 2011), p. 96-98.

Watters WA, Grotzinger JP (2001) Digital reconstruction of calcified early metazoans, terminal Proterozoic Nama Group, Namibia. *Paleobiology* **27**, 1, 159-171.

Whiteman HH, Wissinger SA, Denoël M, Mecklin CJ, Gerlanc NM, Gutrich JJ (2012) Larval growth in polyphenic salamanders: making the best of a bad lot. *Oecologia* **168**, 109-118.

Wood RA (2011) Paleoecology of the earliest skeletal metazoan communities: Implications for early biomineralization. *Earth-Science Reviews*, **106**, 184-190.

Wood RA, Grotzinger JP, Dickson JAD (2002) Proterozoic modular biomineralized metazoan from the Nama Group, Namibia. *Science*, **296**, 2383-2386.

Wood RA, Curtis A (2015) Extensive metazoan reefs from the Ediacaran Nama Group, Namibia: the rise of benthic suspension feeding. *Geobiology*, **13**, 112-122.

Wood RA, Poulton SW, Prave AR, Hoffmann K-H, Clarkson MO, Guilbaud R, Lyne JW, Tostevin R, Bowyer F, Penny AM, Curtis A, Kasemann SA (2015) Dynamic redox conditions control late Ediacaran ecosystems in the Nama Group, Namibia. *Precambrian Research,* **261**, 252-271.

Zhuravlev AYu (2001) Paleoecology of Cambrian reef ecosystems. In: *The History and Sedimentology of Ancient Reef Systems. Topics in Geobiology* (ed. Stanley JD Jr), Plenum Press, pp. 121-157.

Zhuravlev AYu, Wood R (1995) Lower Cambrian reefal cryptic communities. *Palaeontology* **38**, 443-470.

Zhuravlev AYu, Wood RA, Penny AM (2015a) Ediacaran skeletal metazoan interpreted as a lophophorate. *Proceedings of the Royal Society B*, **282**, 20151860

Zhuravlev AYu, Naimark EB, Wood RA (2015b) Control on the diversity and structure of earliest metazoan communities: Early Cambrian reefs from Siberia. *Earth-Science Reviews* **147**, 18-29.

Zieritz A, Aldridge DC (2009) Identification of ecophenotypic trends within three European freshwater mussel species (Bivalvia: Unionoida) using traditional and modern morphometric techniques. *Biological Journal of the Linnean Society,* **98**, 814-825.

TABLE AND FIGURE CAPTIONS

Table 1. Table showing localities sampled, stratigraphic position, dominant lithology and inferred ramp setting. Redox data and interpretations from Wood et al. (2015).

Figure 1. Geological map showing the Nama Group, Namibia (after Grotzinger et al., 2000).

Figure 2. Stratigraphy of the Zaris and Witputs Subbasins and Nama Basin palaeotopography. A – Locality abbreviations and palaeoenvironments at each one. B - Nama Basin paleotopography from Wood et al. (2015). C - Stratigraphy of the Zaris subbasin. D – Stratigraphy of the Witputs subbasin. Generalised stratigraphy and ash bed dates from Grotzinger et al. (2000), Hall et al. (2013), Schmitz (2012), and Saylor et al. (1995, 1998). Abbreviations: U. Mbr = Urikos Member; Z. Fm = Zaris Formation; OS1 = Zaris Subbasin

Sequence Boundary OS1; K1 = Witputs Subbasin Sequence boundary K1; S1 = Witputs Subbasin Sequence boundary S1, PC-C = Precambrian-Cambrian boundary.

Figure 3. Fossil occurrences and inferred redox conditions at the five study localities in the Nama Group. Redox conditions inferred from iron speciation, total iron and total organic carbon measurements in carbonates and shales. Modified from Wood et al. (2015).

Figure 4. *Namacalathus* in low energy inner ramp settings in the Nama Group. A – View on a bedding plane showing *Namacalathus*. Lack of breakage suggests little or no transport, and these may be in life position, with vertical sections provided by toppled individuals. B – View on a bedding plane showing an aggregation. Rare wall deflections may result from close-packed growth, and suggest that these individuals are in growth position. Occasionally smaller individuals occur within larger ones, which may be a result of asexual budding (white arrow). C – Two small *Namacalathus*. The individual to the right shows a stem embedded in thin, undulating laminae.

Figure 5**.** *Namacalathus* in mid-ramp reefs in the Nama Group. A –Transverse section of the cup of a large *Namacalathus* individual containing at least four smaller individuals, one of which has an apparent attachment to the inner cup surface of the larger individual (arrow). B = Botryoidal early cement, S = Sparry late cement. B – View down on a bedding plane showing *Namacalathus* occupying depressions between thrombolite heads, in the 'thombolite associated' palaeoecological habitat. C – Small *Namacalathus* attached to the ceiling of a reef crypt (white arrows). The original crypt is defined by large crystals of dark, early aragonite cement, now neomorphosed to calcite (Wood & Curtis, 2015). D – Closely aggregated *Namacalathus* of uniform size, forming a metre-scale aggregation on an open surface (Wood

& Curtis, 2015). E – *Namacalathus* intergrowing with *Cloudina riemkeae* to form metre-scale reefs (Wood & Curtis, 2015). F – A thicket of thrombolite-associated *Namacalathus*. G – Detail of *Namacalathus* in an open surface aggregation.

Figure 6. *Namacalathus* from an outer ramp setting. A - Aggregated individuals in the outer ramp. B – Two small *Namacalathus* with geopetal infills showing that these examples remained in-situ while micrite was deposited within them. A well-preserved stem is anchored within microbial mat (arrow). C – Small, monospecific, lenticular aggregation enclosed in microbially bound micrite in outer ramp setting. D – Enlargement of C showing *Namacalathus* stems attached to other individuals or to the substrate (white arrows). E – Enlargement of C showing *Namacalathus* individuals attached to each other by their stems, possibly indicating budding (arrows).

Figure 7. Cup diameter distributions for the entire size dataset and for vertical and horizontal sections only. Both show a near-lognormal distribution.

Figure 8. A - Box and whisker plots of cup diameter data for *Namacalathus* from three settings, with the mid-ramp reef setting subdivided into three palaeoecological habitats. "Thromb. Association" = Thrombolite association. Whiskers show the range of the data, while upper and lower boundaries of the boxes show the first and third quartiles. Medians are 8.0 mm for inner ramp; 6.9mm for mid-ramp open surfaces, 7.7mm for *Namacalathus* in thrombolite associations, 5.8 mm in cryptic environments; and 4.4 mm for outer ramp. B - Cup height against cup diameter for all individuals in the three settings, with a major axis linear model suggesting a linear relationship. $R^2 = 0.89867$. Data are given in Table SM 7.

Figure 9. Composite schematic transect placing *Namacalathus* palaeoecologies within a palaeoenvironmental context. Scale bars represent 10mm. A – Inner ramp monospecific aggregations of large *Namacalathus* on a microbially bound micritic substrate. These have the largest median cup diameter of any palaeoenvironment in this study, but not the largest maximum cup diameter. B-E, mid-ramp reef settings. B – Large *Namacalathus* in association with thrombolites. C – Small *Namacalathus* pendant from primary crypt ceilings. D - Thrombolite association of individuals of various cup diameters, with long stems. Smaller individuals appear to be attached to the inner cup surfaces of the larger individuals. E – *Namacalathus* intergrowing with *Cloudina riemkeae* to form metre-scale reefs on open surfaces. F – Small aggregations of small *Namacalathus* on a microbially bound substrate in outer ramp setting, with small individuals attached to, or budding from, pre-existing ones.

Locality	Stratigraphy	Dominant Lithology	Ramp Setting	Redox Data			Redox State
				Fe/Al	Fe_T (wt.%)	Fe_{HR}/Fe_T	
Omkyk Farm	Omkyk Member	Flaggy limestone and dolomitised wackstone and packstone	Inner Ramp	0.612-4.198	0.02-2.66	0.17-1.00	Predominantly anoxic, with fleeting oxia
Zebra River	Omkyk Member	Flaggy limestone and dolomitised wackstone and packstone, microbialite reefs	Inner Ramp	0.45-5.30	0.032-5.279	0.031-0.876	Predominantly anoxic, with fleeting oxia
Pinnacle Reefs	Feldschuhhorn Member	Microbialite reefs	Mid-Ramp	No data	0.042-5.366	0.043-0.253	Probably persistently oxic
Driedoornvlagte	Upper Omkyk Member	Microbialite reefs	Mid-Ramp	No data	0.005-0.383	Not measurable as Fe_T < 0.5wt.%	Probably persistently oxic
Swartpunt	Spitzkopf Member	Lenses of wackstone and packstone	Outer Ramp	No data	0.057-5.544	0.062-0.605	Probable oxic conditions predominate at level of *Namacalathus*; possible brief episodes of anoxia towards top of section (above *Namacalathus* occurrence).

TABLE 1

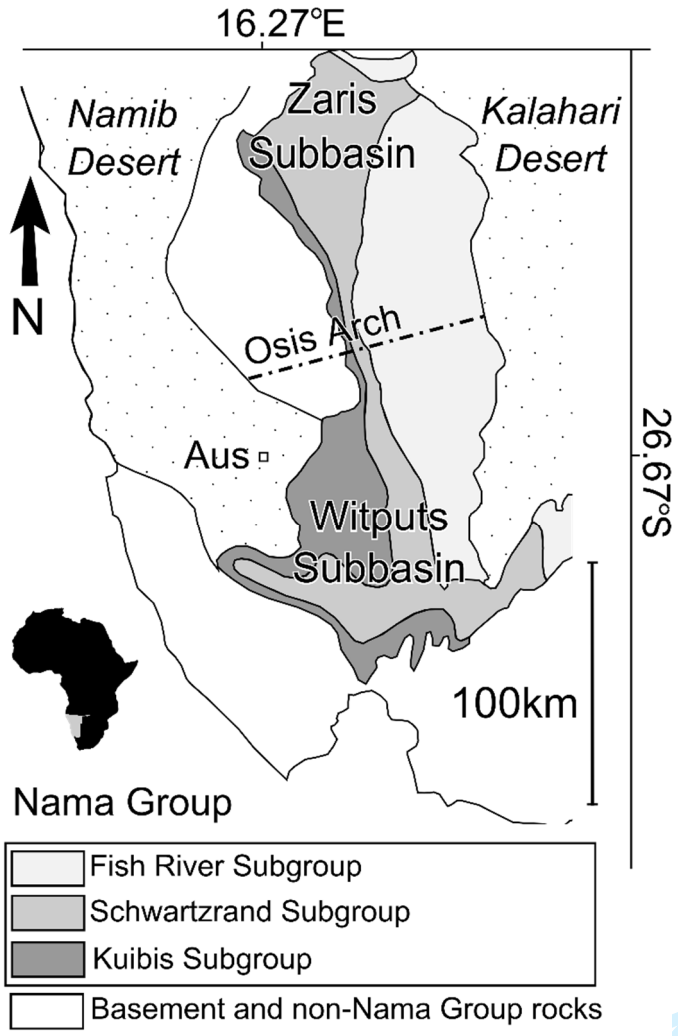
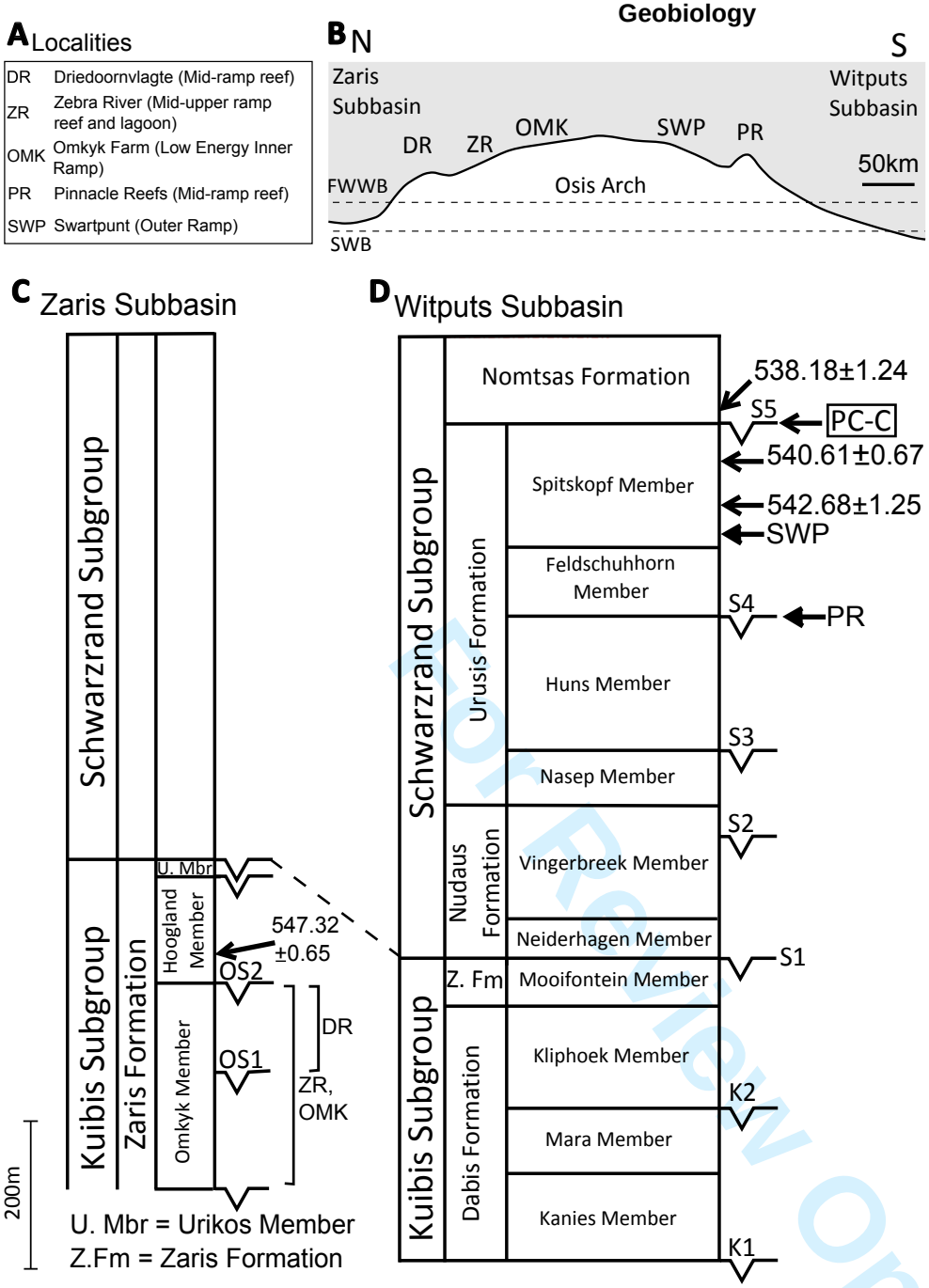
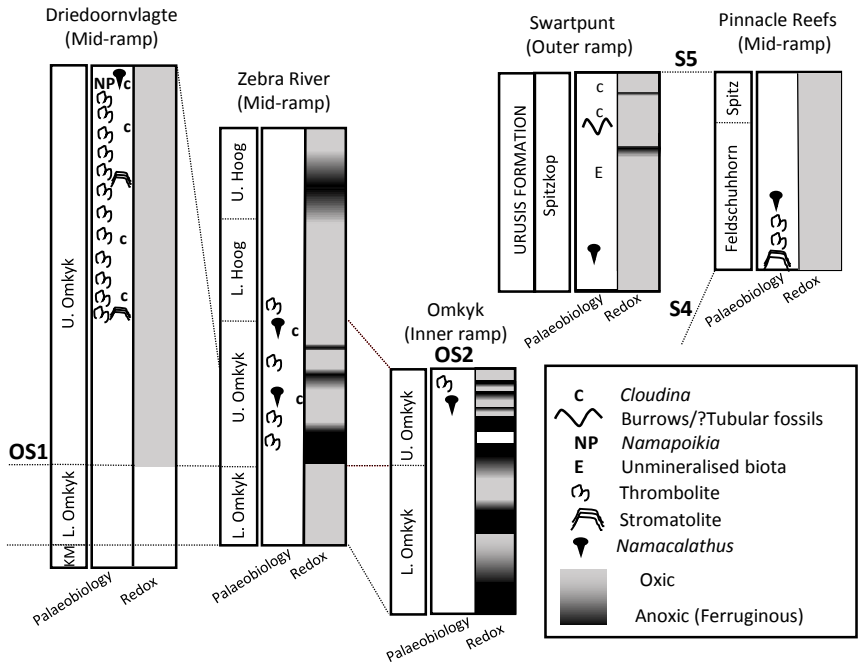
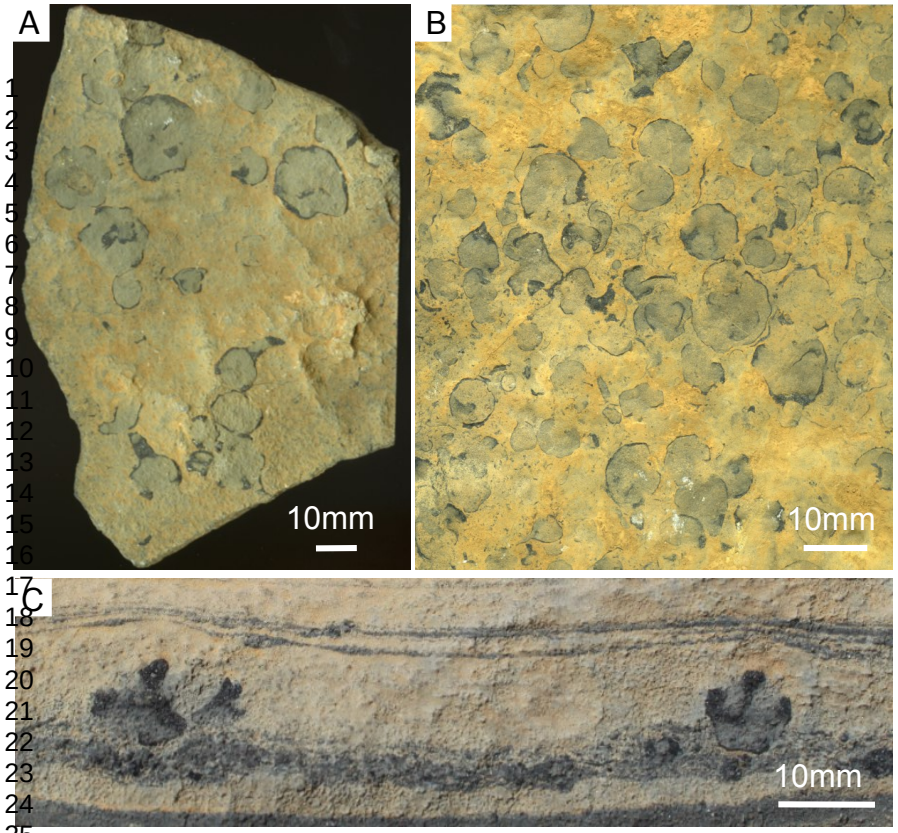
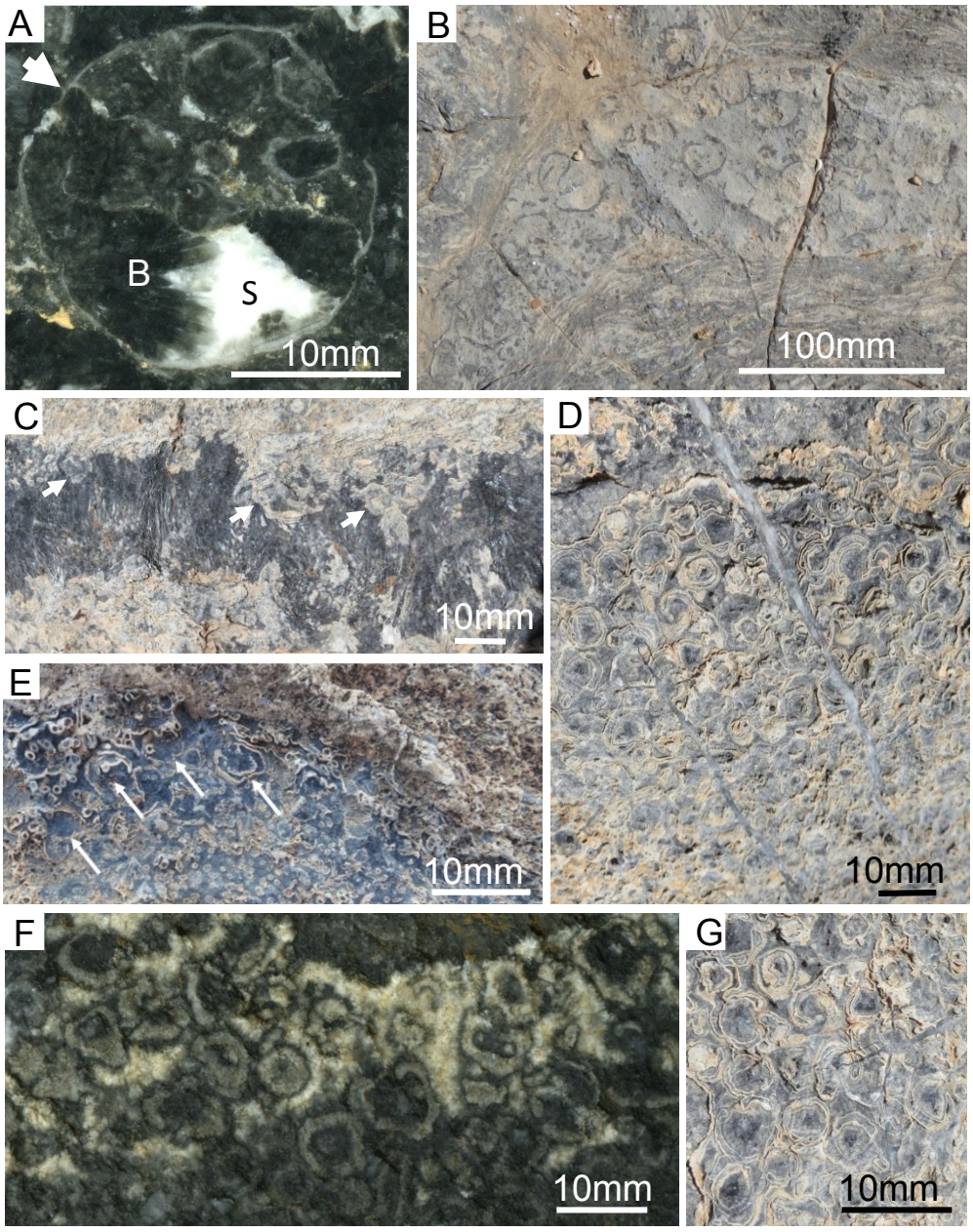


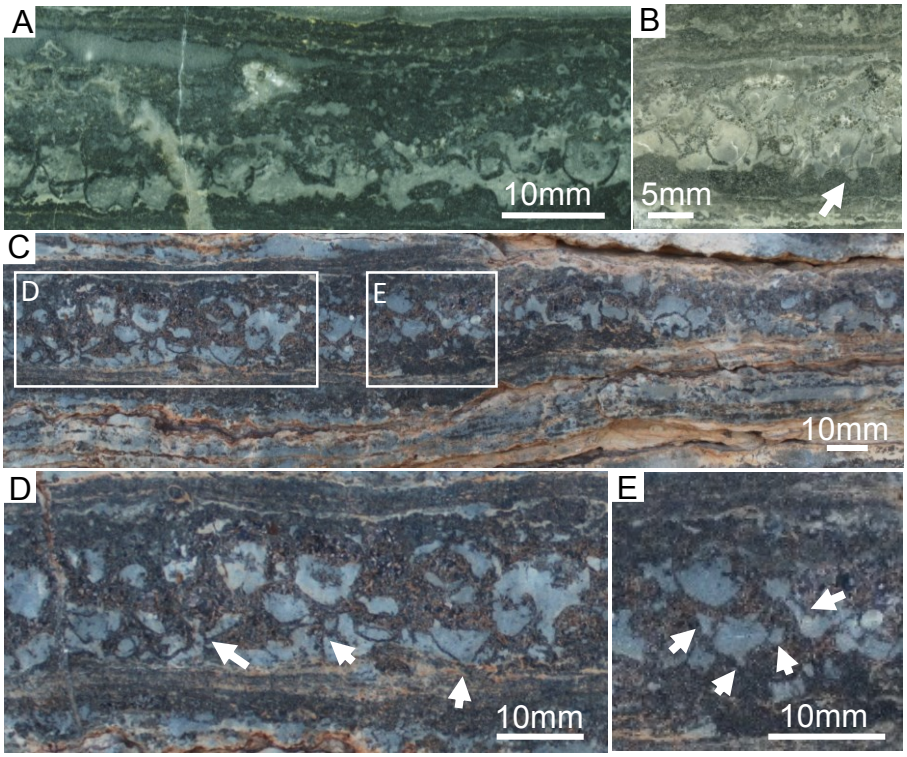
Figure 1




Driedoornvlagte
(Mid-ramp)
U. Omkyk
L. Omkyk
KVE
NP
C
OS1
Palaeobiology
Redox
Zebra River
(Mid-ramp)
U. Hoog
L. Hoog
U. Omkyk
L. Omkyk
Palaeobiology
Redox
Omkyk
(Inner ramp)
OS2
U. Omkyk
L. Omkyk
Palaeobiology
Redox
Swartpunt
(Outer ramp)
URUSIS FORMATION
Spitzkop
C
E
S4
Palaeobiology
Redox
Pinnacle Reefs
(Mid-ramp)
S5
Spitz
Feldschuhhorn
C Cloudina
Burrows/?Tubular fossils
NP Namapoikia
E Unmineralised biota
Thrombolite
Stromatolite
Namacalathus
Oxic
Anoxic (Ferruginous)


A
10mm
B
10mm
C
10mm


A
B
S
10mm
B
100mm
C
10mm
D
10mm
E
10mm
F
10mm
G
10mm


A
10mm
B
5mm
C
D
E
10mm
D
10mm
E
10mm

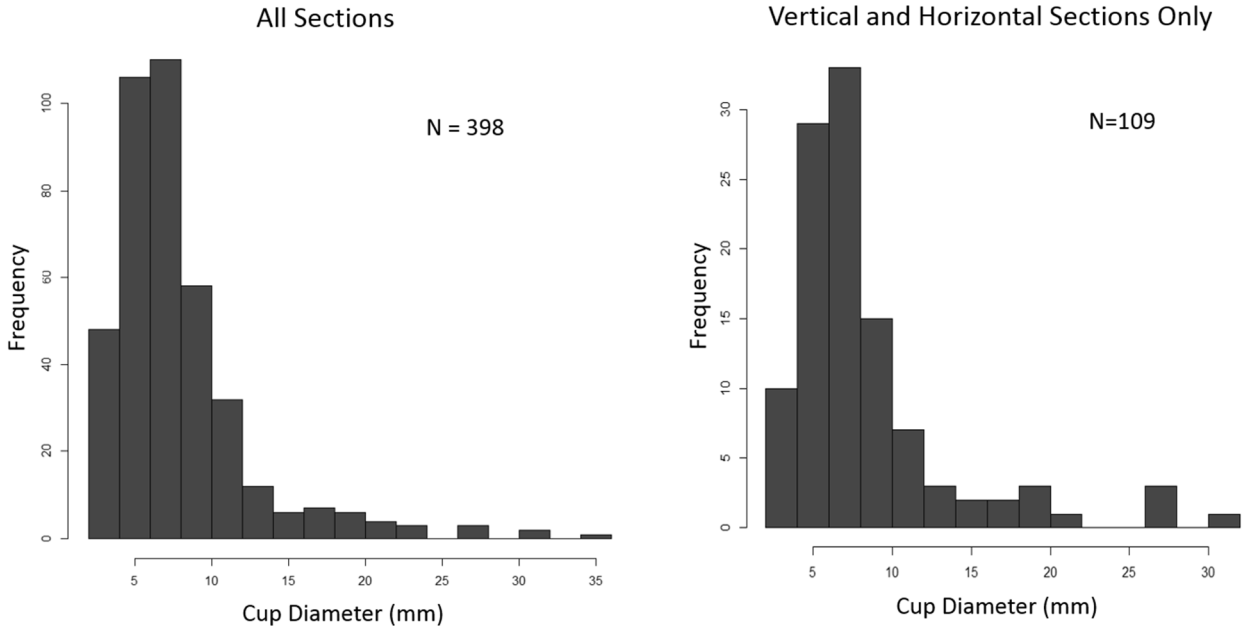
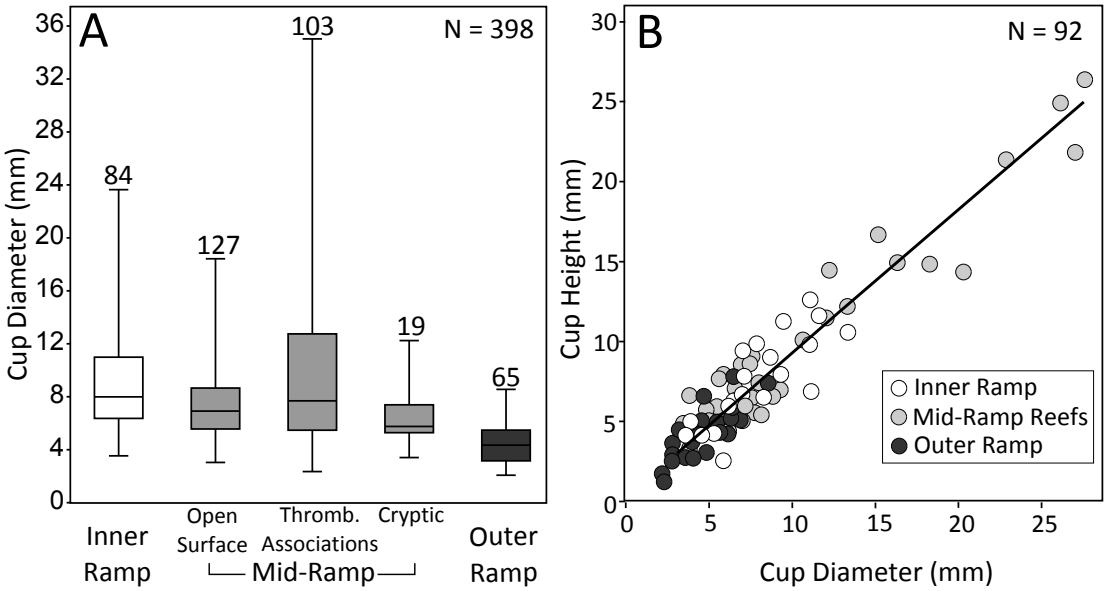


Figure 7



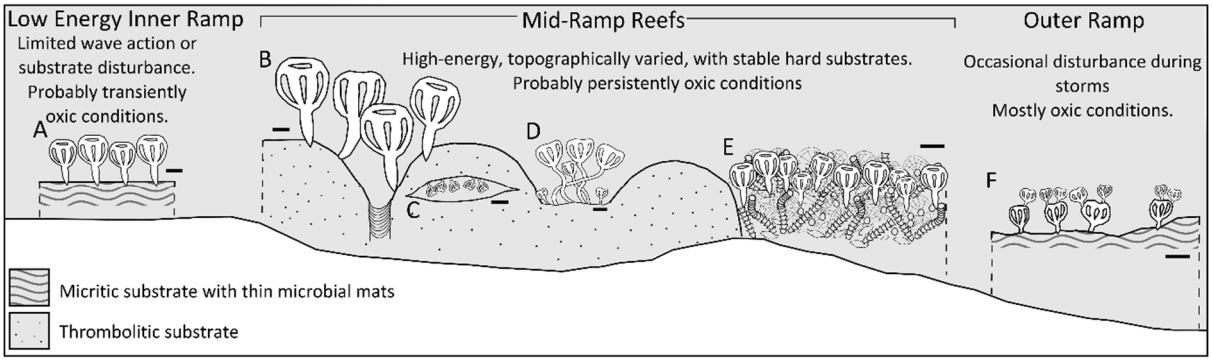


Figure 9